

Behavioral Model for *Homalodisca vitripennis* (Hemiptera: Cicadellidae): Optimization of Host Plant Utilization and Management Implications

R. F. MIZELL, III,^{1,2} C. TIPPING,³ P. C. ANDERSEN,¹ B. V. BRODBECK,¹ W. B. HUNTER,⁴
AND T. NORTHFIELD⁵

Environ. Entomol. 37(5): 1049–1062 (2008)

ABSTRACT The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), (Hemiptera: Cicadellidae), is a xylophagous leafhopper native to the southeastern United States and northern Mexico, with recent introductions into California, Arizona, French Polynesia, and Hawaii. It is a primary vector of the xylem-limited bacterium, *Xylella fastidiosa* Wells et al., the causative agent of Pierce's disease of grape, citrus variegated chlorosis, phony peach, and numerous leaf scorch diseases. *H. vitripennis* uses several hundred species of host plants for feeding, development, and reproduction. Variation in host utilization allows *H. vitripennis* to respond to diurnal and seasonal changes in its nutrient-poor food source, xylem fluid, as well as changing nutritional requirements of each leafhopper developmental stage. Here we provide a conceptual model that integrates behavior, life history strategies, and their associated risks with the nutritional requirements of adult and nymphal stages of *H. vitripennis*. The model is a useful heuristic tool that explains patterns of host plant use, describes insect behavior and ecology, suggests new associations among the ecological components, and most importantly, identifies and supports the development of suppression strategies for *X. fastidiosa* aimed at reducing vector populations through habitat manipulation.

KEY WORDS glassy-winged sharpshooter, behavior, management, *Xylella fastidiosa*

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is a xylem-feeding leafhopper native to the southeastern United States and regions of northern Mexico (Turner and Pollard 1959). This insect is an important vector of the xylem-limited bacterium, *Xylella fastidiosa* (Wells et al. 1987). The bacterium is the causal agent for many economically-important plant diseases including Pierce's disease of grape, phony peach disease, and numerous leaf scald and scorch diseases affecting plum, almond, sycamore, oak, and elm (Timmer et al. 1983, Hopkins and Purcell 2002). Strains of *X. fastidiosa* in South America are responsible for coffee leaf scorch and citrus variegated chlorosis (Lopes et al. 2003). Recent, accidental introductions of *H. vitripennis* into regions of California (Sorenson and Gill 1996), Arizona, French Polynesia (Grandigard et al. 2006), and Hawaii (Almeida 2007) are of great concern because this leafhopper is long-lived and highly polyphagous, and nymphs and adults

are capable of transmitting *X. fastidiosa* to myriad plant species. In its native and introduced range, *H. vitripennis* adults may use >100 species of plants (Turner and Pollard 1959, Adlerz 1980, Mizell and French 1987, Hoddle et al. 2003). Many of these host plant species are important agricultural and horticultural commodities (Bethke et al. 2001). Millions of dollars have been spent for research, suppression, and containment of this invasive vector (Gleeson et al. 2004). Here we present a behavioral model to facilitate understanding and management of *H. vitripennis*.

Diet. The diet of *H. vitripennis* consists exclusively of nutrient-poor xylem fluid (Andersen et al. 1989, 1992, Brodbeck et al. 1993). Xylem fluid is comprised of >98% water and has the most dilute concentrations of dietary nitrogen and carbon of any plant tissue (Raven 1983). Typically, the major organic constituents found in xylem fluid in monomeric form are 19 protein amino acids, 5–7 organic acids, and at least 3 primary sugars (Pate 1980, Andersen et al. 1989, 1992). The amino acid composition of xylem fluid is relatively conserved among many plant species; however, differences in the ratios of these constituents are well documented (Andersen et al. 1989, 1992, 1993, Brodbeck et al. 1996, Bi et al. 2005, Fritschi et al. 2007). The composition of xylem fluid varies between plant species and within an individual plant relating to phenology (Andersen et al. 1992, 1995). In addition, xylem

¹ NFREC-Quincy, University of Florida, 155 Research Rd., Quincy, FL 32351.

² Corresponding author, e-mail: rfmizell@ufl.edu.

³ Delaware Valley College, 700 E. Butler Ave., Doylestown, PA 18901.

⁴ U.S. Horticultural Research Laboratory, 2001 South Rock Rd., Ft. Pierce, FL 34945.

⁵ Department of Entomology, Washington State University, Pullman, WA 99164.

composition is affected by a variety of environmental factors including fertilization, water relations, root-stock, temperature, time of day, and season of the year (Andersen and Brodbeck 1988, 1991, Andersen et al. 1989, 1992, 1995, 2005, Brodbeck et al. 1990).

Feeding Strategies. To successfully develop and reproduce on xylem fluid, *H. vitripennis* has evolved many behavioral and physiological adaptations. These include high consumption rates coupled with efficient nutrient assimilation, host switching, and high vagility of both immature and adult stages (Andersen et al. 1989, 1992, Brodbeck et al. 1993, 1995, 1996, 1999, Blackmer et al. 2003, Tipping et al. 2004). Recent research has identified two species of symbiotic bacteria that occur in *H. vitripennis*, and these symbiotic associations are thought to supplement amino acid or vitamin diet deficiencies (Moran 1998, Wu et al. 2006). Sharpshooters extract xylem fluid with a cibarium that is powered by large dilator muscles, which have their origins in the clypeal region of the head (Ammar 1985). Xylem fluid is under negative tension, and the energy expended during extraction is sometimes only slightly less than the available energy from the constituents of xylem fluid (Andersen et al. 1992). Therefore, high feeding rates are essential to meet nutritional requirements (Andersen et al. 1992). Although perhaps difficult to extract because of the strong tension of water molecules, xylem fluid is mostly devoid of plant secondary compounds that include digestive inhibitors, toxins, and repellents. Xylem fluid is metabolically inexpensive to process because it consists primarily of simple organic compounds, amino acids, and organic acids in monomeric form; therefore, xylem feeders can expend more energy on extraction rather than detoxification (Raven 1983). Additionally, xylem-feeding insects are not water-limited and excrete nitrogenous waste as metabolically inexpensive ammonia. *H. vitripennis* feeding on legumes such as soybean that contain high concentrations of ureides also excrete allantoin and allantoic acid (Brodbeck et al. 1999). Other terrestrial arthropods excrete nitrogenous waste as metabolically expensive but water-conserving uric acid (Brodbeck et al. 1993). Proteins have been found in xylem fluid (Bi et al. 2005), but the scarcity of amino acids in insect excreta that has been hydrolyzed (Andersen et al. 1989) indicates that these compounds are also assimilated with a very high efficiency.

Host Switching. Adult *H. vitripennis* perform optimally on xylem fluid that has higher concentrations of nitrogen-rich amino acids, the amides, which may be important for egg production as well as adult growth and maintenance (Andersen et al. 1992, 2003, 2005, Brodbeck et al. 2004, 2007). Adult females have high consumption rates (note that leafhopper excretion rate is actually measured) (Andersen et al. 1989) when feeding on host plants that contain xylem fluid high in amides and will often oviposit on such plants. However, oviposition on these same hosts may result in 100% mortality of developing nymphs if they remain where they eclose (Brodbeck et al. 1995, 1996, 1999, 2007). The early stage nymphs seek host plants with

balanced amino acid profiles (i.e., profiles with higher relative concentrations of essential amino acids) that are important for successful development (Brodbeck et al. 1993). Similar to adults, older fourth and fifth instars perform well on host plants with a xylem composition that is higher in amides. Studies of artificial diets with other insects indicate that diets consisting of balanced amino acid profiles are more efficiently metabolized (Dadd 1985). A high proportion of a single amino acid in the diet of insects may be unusable or even toxic (Brodbeck and Strong 1987). The adult and immature stages have the ability to disperse, locate, and discriminate between host plants to acquire the resources needed for growth and development, maintenance, and reproduction (Blackmer et al. 2003, Tipping et al. 2004, Park et al. 2005, Coviella et al. 2006). The long-lived *H. vitripennis* rarely persist on a single host plant in greenhouse studies, and it may be similarly uncommon for nymphs to complete their development on only one host plant in the field (Brodbeck et al. 2007). Even in monocultures such as *Citrus* spp. in California where high populations of *H. vitripennis* are common, there are potential weed hosts in the understory (Bi et al. 2005, Park et al. 2005). However, the area of nymph nutrition and associated behaviors needs more field research because nymphal stages can represent a potential bottle neck in the growth and development of *H. vitripennis*. Nymphs can also vector *X. fastidiosa*.

The amides, glutamine and asparagine, are the amino acids most highly correlated with the feeding rates of adult *H. vitripennis* (Andersen et al. 1992, 2005). These amino acids have high nitrogen to carbon ratios and account for much of the caloric value in xylem fluid for most host plants. Other less abundant amino acids were also positively correlated with host abundance and feeding, but the correlations were often less consistent, and the correlation coefficients were lower (Brodbeck et al. 1990, Andersen et al. 1992, 2005). Changes in amino acid profiles within individual plants over time are reflected by changes in *H. vitripennis* abundance and feeding rates. This suggests that the amino acid concentrations, primarily the amides, are responsible for changes in seasonal use of host plants by adults (Adlerz 1980, Mizell and French 1987, Brodbeck et al. 1990). The predominance of amides and their high nitrogen content make them ideal gustatory cues for polyphagous xylem feeders. Amides have also been shown to be phagostimulants for other insects (Albert and Jarret 1981).

Feeding. To compensate for the low nutritional quality of xylem fluid, *H. vitripennis* displays very high consumption rates in comparison with the feeding rates of other insects. Consumption rates by adult *H. vitripennis* of 0.21–0.70 ml/h have been reported on the host plants crape myrtle, *Lagerstroemia indica* L., eastern saltbush, *Baccharis halimifolia* (L.), plum, *Prunus salicina* (Lindl.), soybean, *Glycine max* (L.), and peach, *Prunus persica* (L.) (Andersen et al. 1989, 1992, 2003, 2005, Brodbeck et al. 1995, 1996, 1999, 2007). Hourly consumption rates were \approx 14–50 times dry body weight and were highest during midday on

these species. These relative consumption rates were similar to that reported for two other xylophagous species, *Homalodisca insolita* Walker and *Cuerna costalis* L., when based on body size (Brodbeck et al. 1993). Brodbeck et al. (1993) reported diurnal patterns of feeding rates of *H. vitripennis* caged on crape myrtle and periwinkle, *Cantharanthus roseus* (L.). The nutrient peaks in a greenhouse in crape myrtle and periwinkle occurred during midday and the middle of the night, respectively (Brodbeck et al. 1993). The timing of maximum feeding corresponded closely to the periods of highest amino acid presence in the xylem fluid of the two plant hosts to maximize feeding efficiency.

Assimilation Efficiency. Sharpshooter (Cicadellidae: Cicadellinae) leafhoppers have a high assimilation efficiency of ingested organic compounds relative to other insects (Andersen et al. 1989, Brodbeck et al. 1993). Xylem-feeding leafhoppers possess a long, convoluted midgut equipped with a filter chamber to recirculate ingested xylem fluid and optimize absorption of nutrients (Ammar 1985). The most prevalent amino and organic acids found in the xylem fluid of *L. indica*, *B. halimifolia*, *P. salicina*, and *P. persica* are glutamine, asparagine, arginine, citric, malic, and succinic acid. *H. vitripennis* assimilated >99% of these amino and organic acids. Additionally, the sugars in the xylem of these host plants, glucose, fructose, mannitol, and sorbitol, were also assimilated at >99% efficiency. The calculated potential energy gain from feeding on the xylem fluid of these four host plants was 24.66 ± 5.11 , 17.75 ± 2.01 , 10.01 ± 1.63 , and 3.89 ± 1.38 (SE) J/ml, respectively (Andersen et al. 1989). Andersen et al. (1989) factored the ratios of N ingested and excreted with an estimate of the amount of energy necessary to drive the leafhopper's cibarial feeding pump and determined that *H. vitripennis* derived a net gain in energy from crape myrtle, baccharis, and plum, but suffered a slight net energy loss when forced to feed on peach. Although observations of *H. vitripennis* feeding on potentially suboptimal hosts are common, they most likely remain on these plants for only short time periods, because high mortality occurs to leafhoppers caged on them (Brodbeck et al. 2007). These observations raise questions about the cues that may be used by leafhoppers to make important feeding and movement decisions (Patt and Setamou 2006). Mizell and French (1987) reported the seasonal changes in host plant use in northern Florida and observed that adult *H. vitripennis* were always distributed across a wide array of plants even when most were aggregated on one or a few plant species.

Movement. Host switching is beneficial for xylem-feeding leafhopper survival and enables them to take advantage of the temporal and spatial dynamics of rapidly-changing plant xylem nutrients. Leafhoppers must respond quickly to changes in the xylem fluid content of host plants by dispersing to find adequate nutrients for development, maintenance, and reproduction. Adult *H. vitripennis* are strong fliers and can disperse great distances during their search for opti-

mal host plants (Blackmer et al. 2003). In preliminary studies in northern Florida, a peak feeding and flight time for female *H. vitripennis* occurs between 1000 and 1600 hours (Fig. 1). The time corresponds to when the nutrients in xylem fluid are at their highest in many plants (Andersen et al. 1992, 1995). Although it may seem counterintuitive for leafhoppers to leave a host plant during the time of day when nutrient availability is at a maximum, these nutrient peaks return the most valuable feedback to leafhoppers during the time when they are sampling the nutritional quality of plants to find optimal hosts (Andersen et al. 1992, Brodbeck et al. 1993). Further quantification of *H. vitripennis* flight activity is required.

Although minimal feeding occurs by both sexes in late afternoon and evening (Andersen et al. 1992), interestingly, the flight activity of males increases from dusk until dark (Fig. 1). We have observed that this increased flight activity is related to courtship and mating. Hix (2001) described courtship, associated mating parameters, oviposition, and brochosome application. During this time (1800 hours to dark), males fly haphazardly among the upper branches of host plants. On landing, the males rapidly walk up and down branches in a distinct spiral pattern as they search for receptive females. Brodbeck et al. (1993) reported that *H. vitripennis* reversed its feeding cycle and fed at night when *C. roseus* plants contained the highest xylem fluid nutrient content at night. However, an evening peak in flight often occurs for females during the period when feeding rates are minimal on plants that have low nutrient content at night (Andersen et al. 1992). It is currently not clear if this activity relates to selection of new feeding or ovipositional hosts. Presumably there are substantial rewards for increased evening activity of both males and females, and this behavior would seem to place them at lower risk for predation by dragonflies, Anole' lizards, and spiders that hunt primarily by vision. Further quantification of *H. vitripennis* reproductive behavior is required.

Although wingless, the nymphal stages of *H. vitripennis* are extremely mobile. They have powerful metathoracic legs that enable them to leap several dozen times their body length per jump (e.g., >52 cm) (Tipping et al. 2004). Field studies verify the high vagility of the nymphal instars (Tipping et al. 2004). This behavior may be very important in transmission of *X. fastidiosa* by nymphs.

Oviposition. Female *H. vitripennis* usually insert clusters of eggs into leaf tissue, although we have also observed egg masses on stems and fruits of several species of plants including okra [*Hybiscus esculentus* (L.)], soybean [*Glycine max* (L.) 'D90-9216', and cotton [*Gossypium hirsutum* (L.)] (Tipping et al. 2005). Before oviposition, females use their metathoracic legs to transfer brochosome droplets secreted by the Malpighian tubules onto the forewings, where brochosomes dry as white pellets (Rakitov 2004). During and after oviposition, females rub their metathoracic tibia over the pellets and powder the area where the eggs are inserted into the plant (Rakitov 2004).

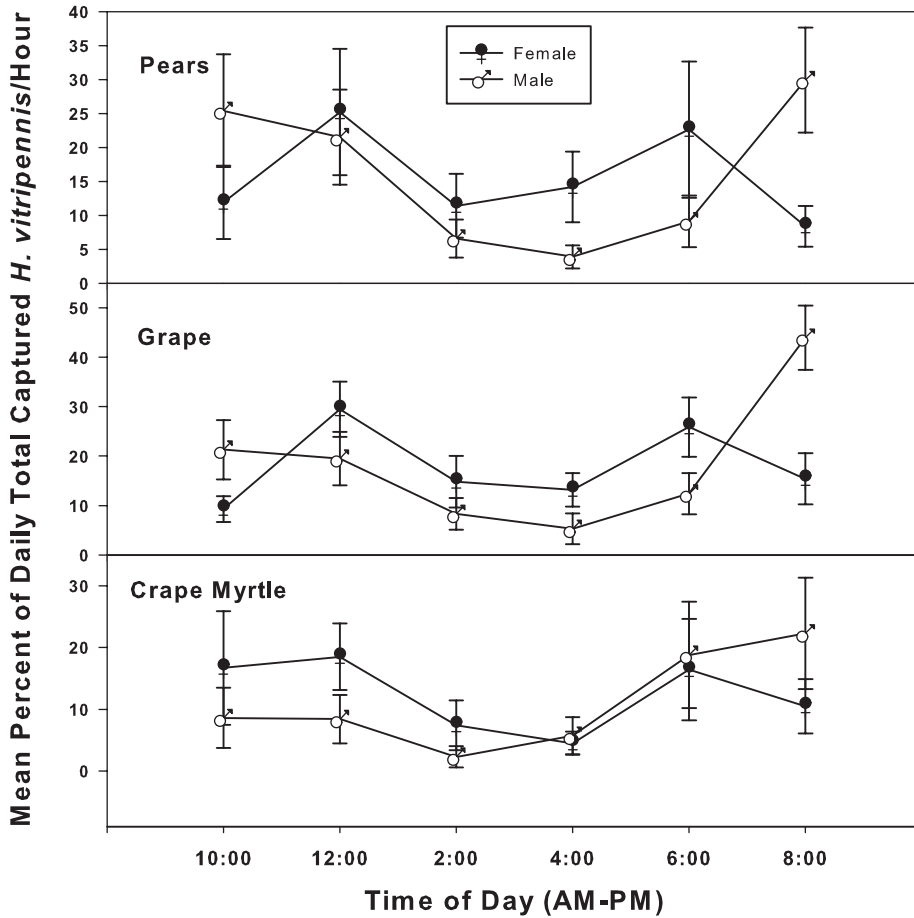


Fig. 1. Mean (\pm SEM) percent of daily total leafhoppers captured per hour over all dates as an indicator of diurnal activity by sex of adult *H. vitripennis* (Germar). Captures are based on yellow trap captures completed in a plantings of grafted 'Flordahome' pear, muscadine grape, *Vitis rotundifolia*, and crape myrtle, *Lagerstroemia indica*, in northern Florida in summer 1988.

Although observations of caged females indicate they will readily oviposit during the daylight hours, oviposition by females in the field predominantly occurs at night (Tipping et al. 2005). The behaviors associated with oviposition and brochosome placement involve jerky movements that are potentially attractive to predators such as spiders and Anole's that use visual or plant vibration cues to find their prey. As females insert their ovipositors into plant tissue, they are not readily able to escape predation by jumping or flying. *H. vitripennis* females oviposit on a large number of host plants and show preferences for certain species both in greenhouse cage studies (Brodbeck et al. 2007) and in the field (Daane and Johnson 2005). However, the important plant criteria and behavioral cues, if any, that are used remain unknown (Irwin and Hoddle 2004). Given the high oviposition rate of *H. vitripennis* (Turner and Pollard 1959) and the potential high level of egg parasitism in Florida and California (Fig. 2) (Triapitsyn et al. 1998, Daane and Johnson 2005, Mizell and Phillips 2005), these ques-

tions concerning behavioral cues need much more research attention (Wise et al. 2008).

Parasitism, Predation, Pathogens, and Reproductive Diapause. In northern Florida and California, egg parasitism by *Gonatocerus* spp. (Mymaridae) is an important mortality factor. Parasitism rates are lower in the spring (Fig. 2), allowing a high number of eggs to hatch. This phenomenon has been observed in both Florida and California (Triapitsyn et al. 1998, Daane and Johnson 2005). However, Hoddle (2006) reported an average of only 19.7% egg parasitism in 2002–2006 in California. Another risk for *H. vitripennis* is the exposure to mummies of the fungus, *Hirsutella homalodisciae*, which remain on the host plants for extended periods. Mummy formation occurs at highest frequency in the fall (Breux 2005), and they repeatedly produce batches of infective spores (Boucias et al. 2007). We have also observed that eggs are widely predated by tree crickets (*Oecanthus* spp.) and earwigs [*Doru taeniatum* (Dohrn)] (R. Lopez and R.F.M., unpublished data).

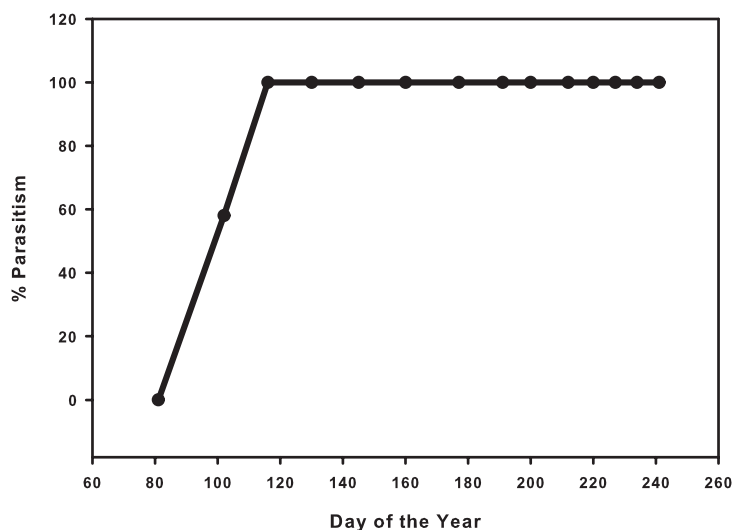


Fig. 2. Weekly percent parasitism of *H. vitripennis* sentinel eggs in 2004 in northern Florida.

Is there enemy-free space to oviposit? We are unaware of any supporting evidence for this phenomenon (see Suttle and Hoddle 2006 for leafhopper effects on predators). Parasitism has been observed in Florida on eggs oviposited in leaves of many plant species including *Citrus* spp., Johnson grass [*Sorghum halepense* (L.) Pers.], redbud (*Cercis canadensis* L.), peach, plum, cotton, soybean, okra, periwinkle, cowpea [*Vigna unguiculata* (L.) Walp], holly (*Ilex* spp.), and crape myrtle (R.F.M., unpublished data). Mizell and Phillips (2005) and Daane and Johnson (2005) reported that all plant species evaluated in several California locations and years did not receive *H. vitripennis* eggs. Host plant species also affects egg parasitism rate (Daane and Johnson 2005). Studies investigating the seasonality of egg parasitism in Florida using weekly sampling with sentinel egg masses indicated low rates of attack early in the spring and nearly complete parasitism during early summer into the fall (Fig. 2). Perhaps enemy-free space occurs during the spring and early summer when populations of parasitoids are low. Additionally, periods of extreme cold temperatures during winter months could reduce early populations of adult parasitoids during the spring, allowing for a greater percentage of *H. vitripennis* eggs to eclose and a subsequent higher number of members of the next generation. This phenomenon of extreme spring population fluctuation would not be unexpected because of the variable nature of the weather conditions in northern Florida. Female *H. vitripennis* begin to enter a reproductive diapause in northern Florida in mid-August, even though abiotic conditions seem optimal for reproduction and an abundance of potential host species are readily available (Table 3).

Female *H. vitripennis* reared from eggs in environmental chambers set to a 13:11 (L:D) photoperiod (23–29°C) entered a reproductive diapause as adults (Table 3). Adult females did not develop mature ova-

ries or produce significant amounts of brochosomes in the Malpighian tubules; however, they did have a large amount of fat body that they acquired (Table 3). This diapause-inducing photoperiod corresponds to 24 August in north Florida. However, only 75% of *H. vitripennis* females reared in chambers set to the photoperiod for 5 August (13.5:10.5 [L:D], 23–29°C) entered reproductive diapause. Perhaps a combination of photoperiod and temperature could be responsible for this physiological phenomenon. By entering a reproductive diapause, regardless of the presence of good reproductive and developmental hosts, females maximize their potential reproductive success by ovipositing in the spring when parasite populations are low and generation times are reduced (Daane et al. 2004).

In fall, generation times are lengthening and the number of quality hosts is decreasing for developing nymphs that may not reach adulthood before cold temperatures occur. However, this hypothesized strategy of avoiding egg parasitoids by an early reproductive diapause is not without risk. The trade-off between diapause and oviposition in a parasite-dense environment may not be equivalent. Diapausing individuals might be exposed to poor environmental conditions associated with severe winter weather including extended periods of subfreezing temperatures and a reduction in the availability of quality hosts required for maintenance. Additionally, the fecundity of leafhoppers that have survived the winter may be reduced because of reduction in lipid reserves and age-associated factors.

During the warmer periods that occur during the winter months, *H. vitripennis* need to feed on metabolically active plants. In the southeastern United States, these most likely include evergreens such as hollies (*Ilex* spp.) or species such as Live oak (*Quercus virginiana* P. Mill.), which only partially defoliate in late spring. Pollard and Kaloostian (1961) reported that *H. vitripennis* are present mainly on oak during the

winter months. In California, *H. vitripennis* frequently overwinters on *Citrus* spp. and *Vitis* spp. (Almeida et al. 2005b). Bi et al. (2005) showed that numbers of overwintering leafhoppers were correlated with xylem nutrient (amino acid) levels. In some rare but pertinent cases, defoliated plants may still be metabolically active at sufficient rates to sustain *H. vitripennis*. For example, Almeida et al. (2005b) reported that *H. vitripennis* overwintered in California on dormant grape *Vitis vinifera* L. with >90% survival.

Strategies of Host Plant Utilization. Optimal foraging theory associates female selection to adult fitness (Jaenike 1986). Theory suggests that foraging phytophagous insects seek food plants that provide the highest return in energy for development, maintenance, and reproduction. Optimal oviposition theory states that oviposition preference will be based on host selection that optimizes the potential performance of offspring (Jaenike 1978, but see Wise et al. 2008); this hypothesis has become the cornerstone of much of the recent literature associated with host selection by phytophagous insects.

Host selection by *H. vitripennis* presents the interesting scenario where optimal foraging and optimal oviposition theory are incongruous (also see Sheirs et al. 2000, Sheirs 2002). Because nutritional requirements of *H. vitripennis* vary with stage of development (Brodbeck et al. 1995, 1996), host selection must favor either optimizing adult performance (optimal foraging theory) or progeny performance (optimal oviposition theory). Although host selection by *H. vitripennis* merits further study (Patt and Setamou 2006), the existing evidence suggests that optimal foraging is more important than oviposition choice in explaining the distribution of adult *H. vitripennis* (Brodbeck et al. 2007). *H. vitripennis* consistently and preferentially selected hosts that resulted in improved aspects of adult performance, while largely ignoring hosts most beneficial to progeny development (Brodbeck et al. 2007). These results are consistent with field observations (Mizell and French 1987). Within the native host range of *H. vitripennis*, *L. indica* is probably the most common summer host for leafhopper adults (Mizell and French 1987, Andersen et al. 1992, Brodbeck et al. 1990), yet proportionally fewer eggs and only later-stage nymphs and adults are found on this host. Other hosts that have been shown to be only marginally suitable for adult *H. vitripennis* such as *Euonymus japonica* will often have much higher abundances of eggs and young nymphs despite low residence time and foraging (Brodbeck et al. 1995). Interestingly, herbaceous legumes have become a common host used by researchers for rearing *H. vitripennis* because of the high success of young nymphs (Brodbeck et al. 2004, Setamou and Jones 2005), yet we are not aware of any reports of adults aggregating in high densities on such hosts in the field.

Other insect species exhibiting a weak linkage between adult preference and progeny performance have been shown to have similarities in life history characteristics including broad host ranges, nonspecific oviposition, and high larval mobility (Pires et al.

2000, Wise et al. 2008). Clearly, all of these characteristics apply to *H. vitripennis*. Xylophagous leafhoppers need to search to locate optimal host plants for development, maintenance, and reproduction because of the dynamic nature of their diet. Organisms that feed on diets that are highly variable have a greater need for increased foraging relative to organisms that require static diets (Real and Caraco 1986). Because xylem fluid is often a nutrient-poor resource in time and in space, xylem feeders are required to disperse to find optimal host plants. They are often large and have increased efficiency in locomotion (Novotny and Wilson 1997), and can quickly assess the quality of a potential host plant (Northfield et al. 2008). Insects with a weak relationship between adult preference and progeny performance often exhibit severe population fluctuations and thus have been deemed "eruptive species," (Price et al. 1990, Price 1994); this terminology may be particularly applicable to *H. vitripennis* given recent outbreaks in California, Arizona, Hawaii, and French Polynesia (Redak et al. 2004, Grandigard et al. 2006, Almeida 2007).

Risks and Trade-offs. The trade-offs associated with decisions by *H. vitripennis* to disperse or to remain on a particular host plant maximize potential fitness (Ronce 2007). Development, maintenance, mating, and fecundity are balanced against starvation, predation, and parasitism. Dispersal seems essential for both the nymphs and the adults. However, dispersal to find optimal hosts is not without costs (Ronce 2007). Leaving a host plant of suboptimal quality offers no assurance that a more suitable host plant will be found. Northfield et al. (2008) discovered that the perceptual range (the distance from which insects can detect hosts) (Lima and Zollner 1996) of response by *H. vitripennis* to locate distant host plants in the landscape was <96 m. Individuals that are forced to migrate by walking or flying are at increased risk of predation. With the exception of spiders that capture prey with silken snares (Tipping et al. 2004), the primary predators of the immature and adult stages of *H. vitripennis* locate their prey by visual cues. Predation by spiders is an important mortality factor for *H. vitripennis* nymphs (Tipping et al. 2004). In northern Florida, spiders in the families Salticidae, Agelenidae, Oxyopidae, and Lycosidae readily feed on the nymph and adult stages (Lopes et al. 2003, Tipping et al. 2004). We observed Odonata capturing adult *H. vitripennis* on the wing. One potential risk-reducing behavior that may reduce leafhopper predation while searching and landing on a new, and likely better host, is to respond to congeners already safely present and feeding. This is a subject of current research.

To summarize the risks, *H. vitripennis* nymphs must balance the cost of malnutrition/starvation (longer developmental time, smaller size) on less optimal host plants versus the risk of predation during dispersal to find food for continued development. Reduced nutrition of nymphs may ultimately affect lifetime fecundity through the reduction in egg production by nutritionally-deprived adults. *H. vitripennis* adults must balance reduced lifetime fecundity from remaining on

inferior food hosts (and perhaps oviposition hosts and subsequent egg and nymph mortality) versus the risks from loss of suitable host plants entirely in combination with the increased risk of predation during the required interplant movements.

Materials and Methods and Results

Diurnal Activity by Sex of *H. vitripennis*. Andersen et al. (1992) discussed the diurnal periodicity and the relationships of plant xylem fluid chemistry and physical properties to *H. vitripennis* feeding. Data were also collected by sex on the diurnal flight periodicity of *H. vitripennis* adults in the same field plots (Fig. 1) used by Andersen et al. (1992). The plots were located in Monticello, FL, and consisted of a 0.2-ha plot of 'Flordahome' pear *Pyrus communis*, a 0.4-ha plot of muscadine grapes and *Vitis* hybrids, and a 0.2-ha plot of several cultivars of crape myrtle, *L. indica*. The pears were ≈ 10 yr old and planted on a 10 by 15-m (within - between rows) spacing, and the grapes were ≈ 5 yr old planted in rows 3 m apart between and 5 m within a row and were trained to a bilateral cordon training system. Crape myrtles were ≈ 3 yr old planted on a 3 by 5-m spacing within and between rows, respectively. Seven yellow sticky traps (15 by 30-cm particle board covered with a thin coat of Tanglefoot) were placed in a row 5 m apart and 1 m above ground on wooden stakes down the center of each plot. Traps were checked every 2 h from 0600 to 2200 hours each day for 10 d beginning on 14 June 1988 and ending 1 July 1988. In preliminary studies, we determined that little or no flight activity occurred by *H. vitripennis* at times other than those studied. Sample days were not always continuous, but each day was begun with clean traps. The number of adult *H. vitripennis* was recorded for each trap per plot by sex and removed from the traps. Trap Tanglefoot was freshened and replenished as necessary. Data analysis was accomplished by dividing the total number of leafhoppers captured per plot each day into the number collected at each 2-h time period to obtain the percent of the total leafhoppers captured per trap per hour. Means and SEM were calculated for the 10 sample d by *H. vitripennis* sex and are presented as the diurnal flight activity (Fig. 1).

Observation of Courtship Behavior. A crape myrtle planting of mixed cultivars with typical northern Florida populations of *H. vitripennis* was used. The study was conducted on 5 d in late June 1988 concurrently with the above diurnal trapping experiment as follows. Between 1700 and 1800 hours each day, ≈ 25 female *H. vitripennis* were identified, and the plant was marked as to their position on the crape myrtle stems. During this period, all females were oriented in the typical inverted feeding position with their entire body touching the substrate (Bextine et al. 2005). From 1800 hours until dark each day, observations were made repeatedly by the senior author by cycling through the marked trees observing as many females as possible, (≈ 20 each day) as to body position relative to the substrate and the presence of males nearby. When no males were present, only the female body

orientation was noted, and observation of the next female began. When males were present, observations were continued until the male mated with or left the female. Male behavior was noted as to how they arrived at the branch, how they moved on the branches with and without females, how they responded to females, and how females responded to males. Males flew haphazardly among the crape myrtle branches at the level of the branch tips ≈ 2 –3 m above ground. The males landed and immediately began moving down the branch in a spiral pattern around the branches, regardless of the presence of females. Females assumed only two postures. The sequence of postures suggested two discrete groupings that were also indicative of color, and hence age, of females. One group, $\approx 75\%$ of the females, that appeared older (faded in color, vitellogenic stage of Hummel et al. 2006) or had obvious wing brochomes changed position before or when males landed and began moving on the branch on which they were located. A stereotypical behavior was observed as follows: females elevated their posterior in a 45° angle to the substrate pressing the anterior portion of the head tight to the substrate while holding on to the substrate with the prothoracic legs. At the same time the meso- and metathoracic legs were extended laterally to the sides of the female such that the males were prohibited from mounting them. In some cases, the males passed by females exhibiting such behavior without responding to them, but attempted to mount with females they apparently recognized as congeners. Younger females without brochomes and appearing more reddish in color (apparently receptive to males, the previtellogenic stage of Hummel et al. 2006) maintained the typical feeding posture. When approached by males, they did not move until the male made contact with them at which time mating occurred by $\approx 25\%$ of the couples. If the female did not respond positively to the male after repeated attempts to mount her, the male continued to move up or down the branch or flew to a new branch and continued searching. This searching and flight activity places the males at especially high risk of predation.

Egg Parasitism of *H. vitripennis* in Northern Florida. Cotton and soybean plants were grown from seed to maturity in the greenhouse in 15-cm pots. Plants were placed inside cages for 24 h with mated *H. vitripennis* that had been subjected to a heat treatment to induce oviposition (Tipping et al. 2005). This resulted in plants containing 5–10 *H. vitripennis* egg masses < 24 h in age. The potted plants with egg masses were placed in the field for 15 d near a crape myrtle planting. At the end of the field exposure, leaves and egg masses were checked for parasitoid emergence and the percentage of parasitized eggs per egg mass was recorded. The experiment was conducted each week from March to September 2004. Mean number of parasitized eggs per week was always 100% except for the first week in March (Fig. 2).

Environmental Chamber and Greenhouse Studies of *H. vitripennis* Reared at Different Photoperiods. Cohorts of *H. vitripennis* nymphs were reared on multiple host plants in environmental chambers pro-

Table 1. Environmental chamber and greenhouse studies of *H. vitripennis* reared at different photoperiods (23–29°C) performed from 5 to 30 June (32°C) and 15 Dec. to 28 Jan. (26–32°C)

Photoperiod	n	Ovarioles	Ova	Fatbody	Brochosomes
13:11 (L:D)	18	2	0	3	1
(Aug. 24)	6	2	0	2.5	1
13.5:10.5 (L:D)	15	2	0	2.5–3	1
(Aug. 5)	5	3	2	2.5–3	3
Greenhouse (summer)	15	3	2	2.5–3	3
Greenhouse (winter)	15	2	0	3	1

Ovarioles: 1, not developed; 2, fully developed, no ova; 3, fully developed with ova.
Ova: 0, none; 1, single ova per ovariole; 2, two ova per ovariole.
Fatbody: 1, minimal; 2, medium; 3, heavy.
Brochosomes (within Malpighian tubules): 1, small; tubule translucent; 2, medium; tubule filled, opaque white; 3, large, tubule swollen, opaque white.

grammed with 13:11 and 13.5:10.5 (L:D) photoperiods (Tipping et al. 2004). Photophase and scotophase temperatures were maintained at 29 and 23°C, respectively. Adult females from both photoperiod treatments were dissected and evaluated ≈30 d after eclosion (Table 1). All females maintained at the 13:11 photoperiod were in reproductive diapause. One third of the females maintained at the 13.5:10.5 photoperiod were reproductively active with mature ova and heavy brochosomes. In another experiment, overwintering, nonreproducing *H. vitripennis* were maintained in screen cages with multiple host plants that were in a greenhouse at ambient light and temperature. On 20 January 2004, six cohorts of two male and female leafhoppers were placed into an environmental chamber with a programmed photoperiod of 11:13 L:D (15°C) for 21 d. Surviving leafhoppers were moved to a greenhouse under summer conditions (14:10 L:D, 29°C). After 12–14 d, brochosomes were observed on the forewings of many of the females. Oviposition followed 1 or 2 d later. Females that are in reproductive diapause can thus be manipulated into becoming reproductively active, and the critical photoperiod for initiation of reproductive diapause in *H. vitripennis* seems to be some combination of a photophase of <13.5 h and a scotophase of >10.5 h.

Table 2. The potential host plant types and their use by *H. vitripennis* and its egg parasitoids along with the potential habitat manipulations to suppress vector populations in the landscape

Type	Adult	Egg	Nymph	Parasite	Manipulation
Nonhost	N	Y/N	Y/N	Y/N	Increase
Primary	Y	Y	Y	Y	Remove
Adult only	Y	Y/N	Y/N	Y/N	Remove or increase as trap crop
Nymph only	N	Y/N	Y	Y/N	Remove
Enemy-free	Y	Y	Y	N	Remove
Suicide	Y	Y	N	Y/N	Increase as trap crop

Multiple options are possible and depicted in each row, e.g., Y/N combinations. Y = yes, the life stage is present or uses the plant, N = no it does not. Combinations are to be summed across rows to provide the plant type under the manipulation column. “Suicide” hosts might occur when no nymphs survived from eggs on such hosts because of host attributes, parasitism, or both.

Discussion

Behavioral Model. A conceptual model of leafhopper behaviors, alternatives, the individual risks (mortality agents), and benefits associated with each behavioral choice is tabulated in Table 1 and depicted in Fig. 5. The derived management implications are presented in Tables 2 and 4. Overwintering behavior is not directly addressed in the model, but is discussed. Although a large amount of information is present in the literature to support this behavioral model, many important *H. vitripennis* behaviors remain to be understood and described. The proposed model is useful to identify new plant/insect associations and is worthwhile to identify avenues of research from which effective management strategies and tactics may be devised.

Descriptions of the conceptual model (Table 1; Fig. 3) will focus on the adult female and her progeny. It begins with the adult female feeding on an optimal host plant essential for production of eggs. As the need to oviposit increases with feeding success, her choices are to remain and oviposit on the plant she is feeding on or to disperse to find another host. If the female remains and oviposits, the nymphs will be initially forced to feed on the host plant from which they eclosed; however, they have the ability to disperse to find other host plants that are essential for survival and development (Brodbeck et al. 1995, Tipping et al. 2004). If the host plant is not acceptable or suboptimal to the adult female for maintenance feeding or egg production, dispersal by the female is likely and will be accompanied by increased risk from predation, exposure to pathogens (Hunnicuttt et al. 2006, Hunter et al. 2006, Boucias et al. 2007), and the risk of not finding a host plant of equivalent or higher quality. The life time fecundity of *H. vitripennis* is >1,000 eggs over a period of >1 yr (Turner and Pollard 1959). Therefore, fitness attributable to egg production is directly related to the female’s continuous ability to locate and choose quality host plants (Ronce 2007). This searching process results in the sampling of a great variety of plants and explains the observed distributions of *H. vitripennis* across a wide variety of plant species. Andersen et al. (1992) showed that nutrient availability changed with plant water status. Lower irrigation levels reduced plant nutrient concentrations, providing further evidence for development and perhaps

Table 3. Behavioral decisions and related risk or mortality factors involved in the biology of the life stages of *H. vitripennis* and other leafhopper vectors

Life stage	Sex	Decisions/actions	Key needs	Mortality factors
Adult	F, M	Taste—move	Nutrients, females (M)	Dis, HPlt, Pred
Adult	F, M	Feed—move	Nutrients, females (M)	Dis, HPlt, Pred
Adult	F	Feed—oviposit	Leaf physical characteristics	Dis, Mal/St, Par, Pred
Adult	F	Move—oviposit	Leaf physical characteristics	Dis, HPlt, Mal/St, Par, Pred
Adult	F, M	Move—feed	Nutrients	Dis, HPlt, Pred
Adult	M	Move—mate		Dis, HPlt, Pred
Nymph (early instar)	F, M	Taste/feed—move	Balanced nutrient profile	Dis, HPlt, Mal/St, Pred
Nymph (late instars)	F, M	Taste/feed—move	Nutrients—high	Dis, Mal/St, Pred
Nymph	F, M	Move	Nutrients	Dis, Pred

Host plant quality refers to adults and malnutrition to nymphs.
M, male; F, female; Dis, disease; HPlt, host plant quality; Mal, malnutrition; Par, parasitism; Pred, predation; St, starvation.

cultural manipulation of management tactics aimed at this disease vector. It seems that the acceptance and rejection of a host plant for feeding by *H. vitripennis* occurs rapidly based on cues about the available nutrient profile directly from the xylem tissue (Brodbeck et al. 1993, Leopold et al. 2003, Backus et al. 2006, Patt and Setamou 2006, Northfield et al. 2008).

Theoretically, once a *H. vitripennis* female locates an optimal host that maximizes fecundity and has suitable oviposition sites, she could remain on the plant for as long as it remains nutritionally adequate and oviposit her entire egg compliment. Eggs are developed and oviposited sequentially in batches of 2–46 (Setamou and Jones 2005). There are some risks associated with this strategy. Placing all eggs in one location invites high parasitism and predation (Fig. 2). A potential counter strategy, masting, is the periodic synchronous production of large numbers of seed by certain tree species to counter predators (Silvertown 1980, Koenig and Knops 2005). Resource pulsing is a more general ecological term for the phenomenon of synchronous production of offspring or emergence in other organisms (Ostfeld and Keesing 2000), such as the emergence of periodical cicadas (Koenig and Liebhold 2005). Hypothetically, it is possible that insects may use a similar strategy to counter natural enemies over shorter time spans. However, parasites seem to be very efficient at finding *H. vitripennis* eggs (Lopez et al. 2003) (Fig. 2), but may be negatively

affected by local temperature regimens (Chen et al. 2006). Additionally, the need by nymphs, especially ones in the early instars with a requisite nutrient profile different than adults, would also decrease the return on such a single-plant or resource-pulsing ovipositional strategy.

The opposite strategy of placing eggs on many diverse and physically suitable host plants seems the more profitable strategy (Robbach et al. 2006). Behaviorally, the plant diversity strategy may be the easiest for females to execute, with oviposition occurring when females are fecund as a secondary behavior of host selection on plants as they are contacted. Plant volatiles produced during oviposition on a variety of species would be more diverse and less likely to provide a consistent cue to be used efficiently by parasites to find eggs. From a nutrient perspective, ovipositing in diverse plant species would present a range of plants available in the future, although unpredictably so, in potentially many different physiological states. This may be the optimal oviposition strategy and a method of bet hedging for adults to enhance the probability for suitable provisions for nymphs whose nutrient requirements are different and change over the course of their development. When offered a diversity of host plants within the confines of 1-m³ cages, *H. vitripennis* oviposited on all hosts available, although preferences were noted (Brodbeck et al. 2007). Moreover, oviposition preferences did not necessarily reflect feeding or residence preferences. These studies suggest *H. vitripennis* is using a diversity strategy in oviposition, although data are needed at the landscape level to confirm this behavior.

Further integration of the concepts of optimal foraging and optimal oviposition is essential to understanding the utilization of host plants by *H. vitripennis*. The influence of xylem nutrients on almost all aspects of *H. vitripennis* life history has been established, with the notable exception being any clear evidence that nutrients affect oviposition choice. Mechanisms of oviposition selection have been proposed and merit further study (Irwin and Hoddle 2004). Selection of ovipositional sites remains the biggest void in understanding host utilization by *H. vitripennis* (Table 1) and hence in formulating strategies for suppression of this important vector.

Table 4. Matrix of plant host types for *X. fastidiosa* after Purcell and Saunders (1999) based on the behavior and movement of the pathogen (left) within individual plant species versus potential use by vectors (top)

	Vector (adult, nymph, oviposition)					
	Poor	Fair	Good	Poor	Fair	Good
	Nonhost					
<i>Xylella fastidiosa</i>	Propagative			Nonpropagative		
	Systemic			Nonsystemic		
	Pathological			Nonpathological		

The use of plant species within these seven *X. fastidiosa* host types for food and oviposition by *H. vitripennis* and other vectors is relatively unknown. Among other uses, such categorizations would provide guidance to managers as to removal or strategic retention or manipulations of individuals of the potentially 21 different *X. fastidiosa*-vector combinations of host types represented for each of the three vector categories of nymph, adult and oviposition.

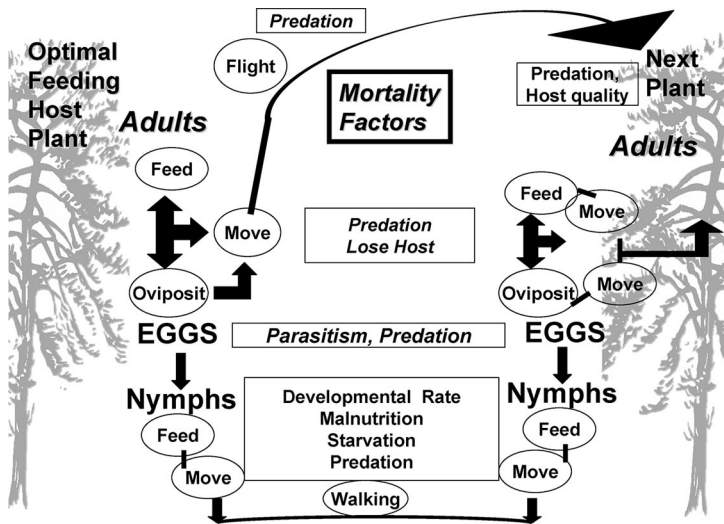


Fig. 3. Behavioral model for *H. vitripennis* (Germar) where the female leafhopper is making decisions at the level of the plant in the context of differential food quality for adults and nymphs and associated risks for each behavioral decision. Bold letters represent the life stages adult, egg, and nymph, ovals are the action choices available, and rectangles are the associated risks, e.g., mortality agents. Begin with adult feeding on an optimal feeding host in the top left corner and work down or across.

Biological control by egg parasitism seems to be a dominant mortality agent. *H. vitripennis* are not proovigenic and are thus time-limited instead of egg-limited (Turner and Pollard 1959). A time-limited species may be less selective in oviposition choice as each egg represents a small percentage of her total reproductive investment; egg-limited species oviposit more optimally (Doak et al. 2006). Therefore, time spent foraging for oviposition hosts is time lost for acquiring nutrients for additional eggs. Although *H. vitripennis* will exhibit preferences in oviposition in cages (Brodbeck et al. 2007), the observed egg deposition in the field on a wide variety of hosts by this species (Daane et al. 2004) is typical of time-limited species (Robb et al. 2006).

Neonates from a single egg mass will eclose within a 20-min period 7–10 d after oviposition depending on environmental conditions (Lopez et al. 2003). They generally remain in the vicinity of the egg mass for 24 h and feed while their cuticle hardens. The neonates are also vulnerable to predation as they move to areas such as small stems or leaf edges that allow them to access xylem tissues. Malnutrition and starvation are leading causes of mortality of immature *H. vitripennis*, and if the host plant does not have a balanced amino acid profile, they can disperse up to several meters a day in search of optimal hosts (Tipping et al. 2004). During dispersal, they are vulnerable to predation. They are also at risk from malnutrition or starvation if they are unable to find adequate host plants. Another potential risk from the movement and host seeking behavior by *H. vitripennis* nymphs and adults is the exposure to spores on leafhoppers mummified by the fungus, *Hirsutella homalodisciae* (Boucias et al. 2007).

The conceptual model, coupled with previous research on vector nutrition and behavior, suggests a number of strategies concerning the use of host plants

to suppress *H. vitripennis* populations at the landscape level (Table 2). Further support is provided by geospatial analyses of the population dynamics of *H. vitripennis* (Park et al. 2005, Northfield et al. 2008). Park et al. (2005) sampled a large area of 450 km² with yellow Seabright traps on a 1.61-km grid of relative low resolution in California. This study concluded that area-wide management of *H. vitripennis* seemed possible because *H. vitripennis* movement and habitat use manifests definite patches and gaps related to host plant types, primarily where *Citrus* spp. is adjacent to *Vitis* spp.

Northfield et al. (2008) similarly trapped an area in northern Florida of 1.61 km² with 52 traps on a 225-m grid, giving a seven times higher resolution of traps within a much smaller area than by Park et al. (2005). Traps used in this study were yellow mailing tubes 7.6 by 30.5 cm placed 1 m above ground. In this study, *H. vitripennis* populations were significantly higher in the eastern half of the experimental plot than the western half that was separated by a 100-m barrier (a road plus grassy margins). Highest populations were found within close proximity to a large planting of cottonwood, an apparently good nymph host, as well as a multispecies irrigated planting of fruit and ornamental species. During 3 yr of sampling, by comparing temporally the relative proportion of trap capture near forested borders to trap capture in the grassy plot interior, *H. vitripennis* populations were found to be higher near the woods in early and late season. This suggests that the movement pattern of *H. vitripennis* is from overwintering quarters in the forest in spring and a return in the fall (Turner and Pollard 1959, Pollard and Kaloostian 1961), and underscores the importance of host plant diversity that provides continuous food quality over the winter season. Both studies (Park et al. 2005, Northfield et al. 2008) documented the im-

portance of quality hosts of different types required by leafhopper adults and nymphs and its relationship to movement and distribution patterns of *H. vitripennis*.

Although suppression of vector populations may have merit, it is the pathogen *X. fastidiosa* that ultimately must be managed. Therefore, the interactions between the vector and pathogen at the level of the host plant are of primary interest (Tubajika et al. 2004, Almeida et al. 2005b). Purcell and Saunders (1999) characterized the potential host plants of *X. fastidiosa* into nonhosts and six infected categories (Table 4). If the specific uses by nymphs for food and adult *H. vitripennis* for food and oviposition (and the egg parasitism rate) of each individual host plant species in these six pathogen host categories were known, these vector host types could be superimposed on the seven pathogen host categories to guide habitat manipulations to better exploit key vector–plant–pathogen interactions (Almeida et al. 2005b).

Table 2 is a hypothetical perspective on the potential utilization of a variety of host plants for *H. vitripennis* coupled with potential effects on the *Gonotocerus* spp. egg parasitoids. This table identifies at least six types of potential host plants and summarizes how use of these plants could be manipulated to reduce populations of *H. vitripennis* by exploiting parasitism or use of other strategies and tactics. Most categories of host plants described are known to exist for *H. vitripennis* (Table 2). Although the model raises the possibility of hosts that provide enemy free space, (i.e., free from egg parasitism) and suicide hosts that will categorically not sustain immature *H. vitripennis*, examples of these host types have not been identified. Addition of selected host types in key locations that enhance parasitism or removal of host types that sustain *H. vitripennis* populations in endemic levels either during the winter or at other times of apparent bottlenecks (droughts, continually in arid land with mosaics of irrigated crop land) may further suppress *H. vitripennis* populations by providing incremental mortality that ultimately leads to local suppression or extinction. Almeida et al. (2005b) discussed other conventional management tactics for *H. vitripennis* and *X. fastidiosa* and host plants that may also be included in this integrated approach.

Gaps still exist in our understanding of the life history of *H. vitripennis*. Adults are highly polyphagous, and eggs may be spread on a wide diversity of hosts, making suppression at these two life stages difficult. However, comparatively few hosts seem adequate for nymph development. Identification and manipulation of nymph hosts has great potential for suppression. The interface between *Citrus* spp. and *Vitis* spp. in California, where a suitable developmental host (*Citrus*) is in close proximity to a good adult host (*Vitis*), illustrates the consequences when the location of host types are not considered or controlled (Blua and Morgan 2003, Bi et al. 2005, Park et al. 2005). Clearly, determining and categorizing hosts as to their uses by *H. vitripennis*, its natural enemies, and *X. fastidiosa*, with due regard for the potential impact on plant physiology of culture and management practices

(Andersen et al. 1995), climate, and weather (Chen et al. 2006, Johnson et al. 2007), and their impacts on vector biology and behavior, offer great potential to manage Pierce's and other *X. fastidiosa* diseases (Table 2) (Purcell and Saunders 1999, Almeida et al. 2005b, Wistrom and Purcell 2005).

Homalodisca vitripennis is easily spread through agricultural commerce and has been detected by regulatory personnel since 1992 in many diverse locations in California (Sorenson and Gill 1996). It has been prohibited or eradicated from many especially sensitive areas including the Napa and Sonoma Valleys. Regulatory actions are most successful when invasive populations are detected before they establish high populations. As a result, the availability of efficient monitoring methods is critical. Central to effective and economical detection is the allocation of traps to areas of high risk for potential invasion and colonization by *H. vitripennis*. Undoubtedly, host plant availability, quality (Table 2), and pattern at the landscape level are important and manageable components affecting *H. vitripennis* distribution and abundance (Blua and Morgan 2003, Park et al. 2005, Northfield et al. 2008). Current detection of *H. vitripennis* relies on inefficient yellow sticky traps. Integration of known vector–host plant interactions to develop a more efficient trap allocation strategy seems warranted. For example, strategic provision of a number of superior host plants in coincidence with trap placement to attract leafhoppers to enhance early detection may not only be a more cost-effective but also a more statistically reliable option.

Conclusions. *Homalodisca vitripennis* seek host plants that have optimal nutritional profiles important to adult fitness, but oviposition behavior remains poorly defined. The location-specific seasonal preferences shown for various host plants by *H. vitripennis* are discrete and predictable (Brodbeck et al. 1990). There is an established physiological basis for this phenomenon: adults can efficiently use nitrogen and carbon from high amide concentrations present in some host plants, whereas young developing nymphs prosper on more balanced nutrient profiles (Brodbeck et al. 1995, 1996, 1999). The trade-off between remaining on a marginal host where leafhoppers are cryptic and have the defensive behavior of hiding behind stems versus dispersal to find better host plants that can increase the risk of predation and disease has not been quantified. Remaining on a poor host plant can lead to reduced fecundity, slower or arrested nymphal development, or reduced size of adults. A longer developmental time could lead to increased exposure of nymphs to predators. Slower development time could also mean the difference between immediately becoming reproductively active or entering a risky reproductive diapause because of the induction of diapause by critical photoperiod, effectively delaying reproduction for a number of months. The behavioral model provides a current synthesis of *H. vitripennis* behavior and ecology and offers a logical perspective for future research. The decisions made, the behavioral cues involved, and the handling of the associated

risks remain to be determined for many observed *H. vitripennis* behaviors. Two obvious needs are a better understanding of *H. vitripennis* oviposition and overwintering behavior. Most importantly, the model provides suggestions for trial and implementation of biologically and behaviorally supported, practical suppression and management strategies and tactics (Almeida et al. 2005a) for the vector and the pathogen using habitat manipulations (Table 2) that may ultimately reduce the incidence of diseases caused by *X. fastidiosa*.

Acknowledgments

We thank M. Blua, R. Groves, J. Lashomb, and anonymous reviewers for helpful comments on previous drafts of the manuscript. We recognize T. C. Riddle and A. Bolques for technical assistance and R. Lopez for insights into various phases of the research. This research was funded in part by several competitive grants to R.F.M. and P.C.A. from the American Vineyard Foundation, the California Department of Food and Agriculture, and the University of California Davis in conjunction with the Glassy-winged Sharpshooter-Pierce's Disease Programs.

References Cited

- Adlerz, W. C. 1980. Ecological observations on two leafhoppers that transmit the Pierce's disease bacterium. *Proc. Fla. State Hort. Soc.* 93: 115-120.
- Albert, P. J., and P. A. Jarret. 1981. Feeding preferences of spruce budworm (*Choristoneura fumiferana* Clem.) larvae to some host plant chemicals. *J. Chem. Ecol.* 7: 391-402.
- Almeida, R. P. 2007. Glassy-winged sharpshooter transmission of *Xylella fastidiosa* to plants. *Proc. HI Entomol. Soc.* 39: 1-4.
- Almeida, R. P., M. J. Blua, J. R. Lopes, and A. H. Purcell. 2005a. Vector transmission of *Xylella fastidiosa*: applying fundamental knowledge to generate disease management strategies. *Ann. Entomol. Soc. Am.* 98: 775-786.
- Almeida, R. P., C. Wistrom, B. Hill, J. Hashim, and A. H. Purcell. 2005b. Vector transmission of *Xylella fastidiosa* to dormant grapes. *Plant Dis.* 89: 419-424.
- Ammar, E. D. 1985. Internal morphology and ultrastructure of leafhoppers and plant-hoppers, pp. 127-163. *In* L. R. Nault and J. G. Rodriguez (eds.), *The leafhoppers and planthoppers*. Wiley, New York.
- Andersen, P. C., and B. V. Brodbeck. 1988. Water and solute flux through pruned spurs of four muscadine grape cultivars. *HortScience* 23: 978-980.
- Andersen, P. C., and B. V. Brodbeck. 1991. Influence of fertilization on xylem fluid chemistry of *Vitis rotundifolia* Noble and *Vitis* hybrid Suwanee. *Am. J. Enol. Vitic.* 42: 245-251.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizell, III. 1989. Metabolism of amino acids, organic acids and sugars extracted from the xylem fluid of four host plants by *Homalodisca coagulata*. *Entomol. Exp. Appl.* 50: 149-159.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizell, III. 1992. Feeding by the leafhopper, *Homalodisca coagulata* in relation to xylem fluid chemistry and tension. *J. Insect Physiol.* 38: 611-622.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizell, III. 1993. Diurnal variations of amino acids and organic acids in xylem fluid from *Lagerstroemia indica*: an endogenous circadian rhythm. *Physiol. Plant.* 89: 783-790.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizell, III. 1995. Diurnal variations in tension, osmolarity, and the composition of nitrogen and carbon assimilates in xylem fluid of *Prunus persica*, *Vitis* hybrid, and *Pyrus communis*. *J. Am. Soc. Hort. Sci.* 120: 600-604.
- Andersen, P. C., B. V. Brodbeck, and R. F. Mizell, III. 2003. Plant and insect characteristics in response to increasing density of *Homalodisca coagulata* on three host species: a quantification of assimilate extraction. *Entomol. Exp. Appl.* 107: 57-68.
- Andersen, P. C., B. V. Brodbeck, R. F. Mizell, III, and S. Oden. 2005. The abundance and feeding of *Homalodisca coagulata* (Hemiptera: Auchenorrhyncha: Cicadellidae) on *Vitis* genotypes in northern Florida. *Environ. Entomol.* 34: 466-478.
- Backus, E. A., J. Habibi, F. Yan, and M. Elleseick. 2006. Stylet penetration by adult *Homalodisca coagulata* on grapes: electrical penetration graph waveform characterization, tissue correlation, and possible implications for transmission of *Xylella fastidiosa*. *Ann. Entomol. Soc. Am.* 98: 787-813.
- Bethke, J. A., M. J. Blua, and R. A. Redak. 2001. Effect of selected insecticides on *Homalodisca coagulata* (Hemiptera: Cicadellidae) and transmission of oleander leaf scorch in a greenhouse study. *J. Econ. Entomol.* 94: 1031-1036.
- Bextine, B. R., B. C. Jackson, D. B. Harshman and T. A. Miller. 2005. *Homalodisca coagulata* (Hemiptera: Cicadellidae) feeding posture. *Ann. Entomol. Soc.* 98: 814-819.
- Bi, J. L., S. J. Castle, F. J. Byrne, S. J. Tuan, and N. C. Toscano. 2005. Influence of seasonal nitrogen nutrition fluctuations in orange and lemon trees on population dynamics of the glassy-winged sharpshooters (*Homalodisca coagulata*). *J. Chem. Ecol.* 31: 2289-2308.
- Blackmer, J. L., J. R. Hagler, G. S. Simmons, and L. A. Canas. 2003. Comparative dispersal of *Homalodisca coagulata* and *Homalodisca liturata* (Hemiptera: Cicadellidae). *Environ. Entomol.* 33: 88-99.
- Blua, M. J., and D. J. Morgan. 2003. Dispersion of *Homalodisca coagulata* (Hemiptera: Cicadellidae), a vector of *Xylella fastidiosa*, into vineyards in southern California. *J. Econ. Entomol.* 96: 1369-1374.
- Boucias, D. G., D. W. Scharf, S. E. Breaux, D. H. Purcell, and R. F. Mizell, III. 2007. Studies on the fungi associated with the glassy-winged sharpshooter *Homalodisca coagulata* with emphasis on a new species *Hirsutella homalodiscae* nom. prov. *Biocontrol* 52: 231-258.
- Breaux, E. 2005. Mycopathogens of the glassy-winged sharpshooter. M.S. thesis, University of Florida, Gainesville, FL 32611.
- Brodbeck, B. V., and D. Strong. 1987. Amino acid nutrition of herbivorous insects and stress to host plants, pp. 347-364. *In* P. Barbosa and J. C. Schultz (eds.), *Insect outbreaks*. Academic, New York.
- Brodbeck, B. V., R. F. Mizell, III, W. J. French, and P. C. Andersen. 1990. Amino acids as determinants of host preference for the xylem feeding leafhopper *Homalodisca coagulata* (Hemiptera: Cicadellidae). *Oecologia (Berl.)* 83: 338-345.
- Brodbeck, B. V., R. F. Mizell, III, and P. C. Andersen. 1993. Physiological and behavioral adaptations of the three species of leafhoppers in response to the dilute nutrient content of xylem fluid. *J. Insect Physiol.* 39: 73-81.
- Brodbeck, B. V., P. C. Andersen, and R. F. Mizell, III. 1995. Differential utilization of nutrients during development by the xylophagous leafhopper, *Homalodisca coagulata*. *Entomol. Exp. Appl.* 75: 279-289.

- Brodbeck, B. V., P. C. Andersen, and R. F. Mizell, III. 1996. Utilization of primary nutrients by the polyphagous xylophage, *Homalodisca coagulata*, reared on single host species. Arch. Insect Biochem. Phys. 32: 65–83.
- Brodbeck, B. V., P. C. Andersen, and R. F. Mizell, III. 1999. Effects of total dietary nitrogen and nitrogen form on the development of xylophagous leafhoppers. Arch. Insect Biochem. Phys. 42: 37–50.
- Brodbeck, B. V., P. C. Andersen, R. F. Mizell, III, and S. Oden. 2004. Comparative nutrition and developmental biology of xylem-feeding leafhoppers reared on four genotypes of *Glycine max*. Environ. Entomol. 33: 165–173.
- Brodbeck, B. V., P. C. Andersen, R. F. Mizell, S. Oden, and R. F. Mizell, III. 2007. Preference-performance linkage of the xylem feeding leafhopper, *Homalodisca vitripennis* (Hemiptera: Cicadellidae). Environ. Entomol. 36: 1512–1522.
- Chen, W., R. A. Leopold, D. J. Morgan, and M. O. Harris. 2006. Development and reproduction of the egg parasitoid *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae), as a function of temperature. Environ. Entomol. 35: 1178–1187.
- Daane, K. M., and M. W. Johnson. 2005. Biology and ecology of the glassy-winged sharpshooter in the San Joaquin Valley. CDFA Pierce's Dis. Res. Sym. Proc. 97–100.
- Daane, K. M., M. W. Johnson, T. Rutz, and J. Hashim. 2004. Host plant influence on glassy-winged sharpshooters and its natural enemies. In Proceedings of the IV California conference on biological control, 13–15 July 2004, Berkeley, CA.
- Dadd, R. H. 1985. Nutrition: organisms, pp. 313–390. In G. A. Kerkut and L. T. Gilbert (eds.), Comprehensive insect physiology, biochemistry and pharmacology. Pergamon, New York.
- Doak, P., P. Kareiva, and J. Kingsolver. 2006. Fitness consequences of choosy oviposition for a time-limited butterfly. Ecology 87: 395–408.
- Fritschi, F. B., J. C. Cabrera-La Rosa, H. Lin, M. W. Johnson, and R. L. Groves. 2007. Behavioral responses of *Homalodisca vitripennis* (Hemiptera: Auchenorrhyncha: Cicadellidae) on four *Vitis* genotypes. Environ. Entomol. 36: 926–927.
- Gleeson, P., J. Dlott, C. Ohmart, and M. Zeiss. 2004. Final report to CDFA: Pierce's disease and glassy-winged sharpshooter research evaluation contract 02–628, January 2003–January 2004. Am. Vineyard Found., Napa, CA 94581.
- Grandigard, J., M. S. Hoddle, G. K. Roderick, J. N. Petit, D. Percy, R. Putoa, C. Garnier, and N. Davies. 2006. Invasion of French Polynesia by the glassy-winged sharpshooter, (Hemiptera: Cicadellidae): a new threat to the South Pacific. Pacific Sci. 60: 429–438.
- Hix, R. L. 2001. Egg-laying and brochosome production observed in glassy-winged sharpshooter. Calif. Agric. 55: 19–22.
- Hoddle, M. S. 2006. Are glassy-winged sharpshooter populations regulated in California? Long-term phenological studies and construction of multi-cohort life tables for the glassy-winged sharpshooter in citrus. CDFA Pierce's Dis. Res. Sym. Proc. 73–75.
- Hoddle, M. S., S. V. Triapitsyn, and D. J. Morgan. 2003. Distribution and plant associations records for (Hemiptera: Cicadellidae) in Florida. Fla. Entomol. 86: 89–91.
- Hopkins, D. L., and A. H. Purcell. 2002. *Xylella fastidiosa*: cause of Pierce's disease of grapevine and other emergent diseases. Plant Dis. 86: 1056–1066.
- Hummel, N. A., F. G. Zalom, N. C. Toscano, P. Burman, and C. Y. Peng. 2006. Seasonal patterns of female *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) Reproductive physiology in Riverside, California. Environ. Entomol. 35: 901–906.
- Hunnicut, L. E., W. B. Hunter, R. D. Cave, C. A. Powell, and J. J. Mozoruk. 2006. Complete genome sequence and molecular characterization of *Homalodisca coagulata* virus-1, a novel virus discovered in the glassy-winged sharpshooter (Hemiptera: Cicadellidae). Virology 350: 67–78.
- Hunter, W. B., C. S. Katsar, and J. X. Chaparro. 2006. Nucleotide sequence of 3'-end of *Homalodisca coagulata* virus-1. A new leafhopper-infecting virus from the glassy-winged sharpshooter. J. Insect Sci. 6: 28.
- Irwin, N. A., and M. S. Hoddle. 2004. Oviposition preference of *Homalodisca coagulata* for two *Citrus limon* cultivars and influence of host plant on parasitism by *Gonatocerus ashmeadi* and *G. triggatus* (Hymenoptera: Mymaridae). Fla. Entomol. 87: 504–510.
- Jaenike, J. 1978. On optimal oviposition behavior in phytophagous insects. Theor. Popul. Biol. 14: 350–356.
- Jaenike, J. 1986. Feeding behavior and future fecundity in *Drosophila*. Am. Nat. 127: 118–123.
- Johnson, M. W., K. M. Daane, R. L. Groves, and E. A. Backus. 2006. Spatial population dynamics and overwintering biology of the glassy-winged sharpshooter in California's San Joaquin Valley. CDFA Pierce's Dis. Res. Sym. Proc. 12–15.
- Johnson, M. W., K. Lynn-Patterson, M. Sisterson, and R. L. Groves. 2007. Assessing the post-winter threat of glassy-winged sharpshooter populations. CDFA Pierce's Dis. Res. Sym. Proc. : 34–37.
- Koenig, W. D., and J. M. Knops. 2005. The mystery of the masting of trees. Am. Sci. 94: 340–347.
- Koenig, W. D., and A. M. Liebhold. 2005. Effects of periodical cicada emergences on abundance and synchrony of avian populations. Ecology 86: 1873–1882.
- Leopold, R., T. Freeman, J. Buckner, and D. Nelson. 2003. Mouthpart morphology and stylet penetration of host plants by the glassy-winged sharpshooter, *Homalodisca coagulata* (Homoptera: Cicadellidae). Arthropod Struct. Dev. 32: 189–199.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Tree 11: 131–135.
- Lopes, J. R., S. Marcussi, C. Torres, V. Souza, C. Fagan, S. Franca, N. Fernandes, and J. Lopes. 2003. Weeds as alternative hosts of the citrus, coffee and plum strains of *Xylella fastidiosa* in Brazil. Plant Dis. 87: 544–549.
- Lopez, R., R. F. Mizell, III, P. C. Andersen, and B. V. Brodbeck. 2003. Impact of natural enemies on populations of the glassy-winged sharpshooter, *Homalodisca coagulata* (Say) in north Florida, pp. 484–486. In R. Van Driesche (ed.), First international symposium on biological control of arthropods. In R. Van Driesche (ed.), Proceedings of the First International Symposium on Biological Control of Arthropods, USDA For. Serv., Morgantown, WV, USA, FHTET-03-05.
- Mizell, R. F., and W. J. French. 1987. Leafhopper vectors of phony peach disease: feeding site preference and survival on infected and uninfected peach, and seasonal response to selected host plants. J. Entomol. Sci. 22: 11–22.
- Mizell, R. F., and P. A. Phillips. 2005. Population dynamics and interactions between glassy-winged sharpshooter and its host plants in response to California phenology. CDFA Pierce's Dis. Res. Sym. Proc. : 117–121.
- Moran, N. A. 1998. Bacterio-cyte-associated symbionts of insects. Bioscience 48: 295–304.

- Northfield, T., R. F. Mizell, III, P. C. Andersen, B. V. Brodbeck, and T. C. Riddle. 2008. Dispersal, patch leaving and aggregation of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae). *Environ. Entomol.* (in press).
- Novotny, V., and M. R. Wilson. 1997. Why are there no small species among xylem-sucking insects? *Evol. Ecol.* 11: 419–437.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* 15: 232–237.
- Park, Y., T. Perring, C. Farrar, and C. Gispert. 2005. Spatial and temporal distributions of two sympatric *Homalodisca* spp. (Hemiptera: Cicadellidae): implications for areawide pest management. *Agric. Ecosyst. Environ.* 113: 168–174.
- Pate, J. S. 1980. Transport partitioning of nitrogenous solutes. *Annu. Rev. Phytopath.* 31: 313–340.
- Patt, J. M., and M. Setamou. 2006. Olfactory and visual stimuli affecting host plant detection in *Homalodisca coagulata* (Hemiptera: Cicadellidae). *Environ. Entomol.* 36: 142–150.
- Pires, C.S.S., P. W. Price, and E. G. Fontes. 2000. Preference-performance linkage in the neotropical spittlebug *Deois flavopicta*, and its relation to the phylogenetic constraints hypothesis. *Ecol. Entomol.* 25: 71–80.
- Pollard, H. N., and G. H. Kaloostian. 1961. Overwintering habits of *Homalodisca coagulata*, the principle natural vector of phony peach disease virus. *J. Econ. Entomol.* 54: 810–811.
- Price, P. W. 1994. Phylogenetic constraints, adaptive syndromes, and emergent properties: from individuals to population dynamics. *Res. Pop. Ecol.* 36: 3–14.
- Price, P. W., T. P. Craig, G.W. Fernandes, J. K. Itami, S. P. Mopper, and R. W. Prezzler. 1990. Insect herbivore population dynamics on herbs and shrubs: new approaches to latent and eruptive species and life table development, pp. 1–38. *In* E. A. Bernays (ed.), *Insect-plant interactions*, vol. I. CRC, Boca Raton, FL.
- Purcell, A. H., and S. Saunders. 1999. Fate of Pierce's disease strains of *Xylella fastidiosa* in common riparian plants in California. *Plant Dis.* 83: 825–830.
- Rakitov, R. A. 2004. Powdering of egg nests with brochosomes and related sexual dimorphism in leafhoppers (Hemiptera: Cicadellidae). *Zool. J. Linn. Soc. Lond.* 140: 353–381.
- Raven, J. A. 1983. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Annu. Rev. Ecol. Syst.* 13: 135–234.
- Real, L., and T. Caraco. 1986. Risk and foraging in stochastic environments. *Annu. Rev. Ecol. Syst.* 17: 371–390.
- Redak, R. A., M. J. Blua, J. R. Lopes, A. H. Purcell, R. F. Mizell, III, and P. C. Andersen. 2004. The biology and control of xylem sap-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annu. Rev. Entomol.* 49: 243–70.
- Robbach, A., B. Lohr, and S. Vidal. 2006. Does a specialist parasitoid adapt to its host on a new host plant? *J. Insect Behav.* 19: 479–495.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Syst.* 38: 231–253.
- Setamou, M., and W. L. Jones. 2005. Biology and biometry of sharpshooter *Homalodisca coagulata* (Hemiptera: Cicadellidae) reared on Cowpea. *Ann. Entomol. Soc. Am.* 98: 322–328.
- Sheirs, J. 2002. Integrating optimal foraging and optimal oviposition theory in plant-insect research. *Oikos* 111: 187–191.
- Sheirs, J., D. Bruyn, and R. Verhagen. 2000. Optimization of adult preference determines host choice in a grass miner. *Proc. R. Soc. Lond.* 267: 2065–2069.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* 14: 235–250.
- Sorenson, S., and R. Gill. 1996. A range extension of *Homalodisca coagulata* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California. *Pan. Pac. Entomol.* 72: 160–161.
- Suttle, K. B., and M. S. Hoddle. 2006. Engineering enemy-free space: an invasive pest that kills its predators. *Biol. Invasions* 8: 639–649.
- Timmer, L. W., R. H. Bransky, R. F. Lee, and B. C. Raju. 1983. A fastidious xylem-limited bacterium infecting ragweed. *Phytopathology* 73: 975–979.
- Tipping, C., and R. F. Mizell, III. 2004. Overwintering biology of the glassy-winged sharpshooter and *Gonatocerus ashmeadi*. *CDFA Pierce's Dis. Res. Sym. Proc.* 153–156.
- Tipping, C., R. F. Mizell, III, and P. C. Andersen. 2004. Dispersal adaptations of immature stages of three species of leafhopper (Hemiptera: Auchenorrhyncha: Cicadellidae). *Fla. Entomol.* 87: 372–379.
- Tipping, C., R. F. Mizell, III, B. V. Brodbeck, P. C. Andersen, W. B. Hunter, and R. Lopez-Gutierrez. 2005. A novel method to induce oviposition of the glassy-winged sharpshooter, *Homalodisca coagulata* (Hemiptera: Auchenorrhyncha: Cicadellidae). *J. Entomol. Sci.* 40:246–249.
- Triapitsyn, S. V., R. F. Mizell, III, and J. L. Bossart. 1998. Egg parasitoids of *Homalodisca coagulata* (Homoptera: Cicadellidae). *Fla. Entomol.* 81: 241–243.
- Tubajika, K., E. Civerolo, M. Ciomperlik, D. Luvisi, and J. Hashim. 2004. Analysis of the spatial patterns of Pierce's disease incidence in the lower San Joaquin Valley in California. *Phytopathology* 94: 1136–1144.
- Turner, W. F., and H. N. Pollard. 1959. Life histories and behaviors of five insect vectors of phony peach disease. *USDA Tech. Bull.* 1188. 28pp.
- Wells, J. M., B. C. Raju, H. Y. Hung, W.G. Weisburg, L. M. Paul, and D. J. Brenner. 1987. *Xylella fastidiosa* gen. nov., sp. nov: gram-negative, xylem-limited, fastidious plant bacteria related to *Xanthomonas* spp. *Int. J. Syst. Bacteriol.* 37: 136–143.
- Wise, M., J. Partelow, K. Everson, M. Anselmo, and W. Abrahamson. 2008. Good mothers, bad mothers, and the nature of resistance to herbivory in *Solidago altissima*. *Oecologia (Berl.)* 155: 257–266.
- Wistrom, C., and A. H. Purcell. 2005. The fate of *Xylella fastidiosa* in vineyard weeds and other hosts in California. *Plant Dis.* 89: 794–799.
- Wu, D., S. C. Daugherty, S. E. van Aken, G. H. Pai, K. L. Watkins, H. Khouri, L. J. Tallon, J. M. Zaborsky, H. E. Dunbar, P. L. Tran, N. A. Moran, and J. A. Elsen. 2006. Metabolic complementarity and genomics of the dual bacterial symbiosis of sharpshooters. *PLOS Biol.* 4: 1079–1092.

Received 7 August 2007; accepted 9 April 2008.